

Full Length Research Paper

Generation mean analysis of dual purpose traits in cowpea (*Vigna unguiculata* [L.] walp)

A. O. Adeyanju^{1*}, M. F. Ishiyaku², C. A. Echekwu² and J. D. Olarewaju²

¹Department of Plant Science, Faculty of Agriculture, Ahmadu Bello University Zaria, Samaru. Kaduna State, Nigeria.

²Department of Plant Science, Institute for Agricultural Research, Ahmadu Bello University Zaria, Samaru. Kaduna State, Nigeria.

Accepted 20 April, 2012

Dual-purpose, the relative ratio of grain to fodder productivity of cowpea (*Vigna unguiculata*) is one of the major factors affecting the adoption of new varieties in sub-Saharan Africa. Efforts have been made to improve either the fodder or the grain productivity separately. However, there is the need to develop a variety with both good grain and fodder productivity. Gene effects for dual-purpose traits were estimated from the combined analysis of the parental, F₁, F₂ and backcross populations involving one fodder cowpea and two grain type cowpeas with the aim of understanding the genetic basis of these characteristics. The fodder parent had significantly better performance compared to the grain types for all dual-purpose traits. Transgressive segregates for high and low fodder yield were observed, suggesting that the fodder yielding genes were dispersed among the parents. Frequency analysis showed that all the F₂ populations for fodder yield exhibited a continuous distribution, suggesting that inheritance of fodder yield is quantitative in nature and may involve more than two genes. Epistatic effects were found to be important for all dual-purpose traits (days to first flower, plant height, pod weight, leaf weight, branch weight, seed weight, biomass and fodder yield). Fodder yield per plant appeared to be influenced by both additive and non-additive gene effects, whereas grain yield was influenced by complementary gene action. Duplicate gene interaction was predominantly involved in the inheritance of most of the structural traits (plant height, leaf weight and branch weight). For genetic improvement of fodder and grain yield, utilizing non-additive components, intermating among selected segregates in early generation or reciprocal recurrent selection should be effective approaches.

Key words: Gene effects, fodder, *Vigna unguiculata*, generation mean analysis.

INTRODUCTION

Cowpea (*Vigna unguiculata*) is of vital importance to the livelihood of millions of people in West and Central Africa. From its production, rural families derive food, animal feed and cash income. It provides nutritious grain and an inexpensive source of protein for both rural poor and urban consumers. Cowpea grain contains about 25% protein and 64% carbohydrate (Bressani 1985) and therefore has a tremendous potential to contribute to the alleviation of malnutrition among resource-poor farmers.

Dual-purpose, the relative ratio of grain to fodder

productivity of cowpea, is one of the major factor affecting the adoption of new varieties in the West African savannas. Efforts have been made to improve either, the fodder or the grain productivity, separately. However, there is the need to develop a variety with both good grain and fodder productivity.

Throughout the developing world, there is an increasing emphasis on integrating crop and livestock production to promote more sustainable agricultural systems. In the dry savannas of West and Central Africa, crop and livestock enterprises are closely integrated. Most farmers in this region keep livestock; therefore cowpea forms an integral part of the cropping system. The cowpea haulm is used to feed the livestock, whereas the latter provides manure

*Corresponding author. E-mail: dayo_ene@yahoo.com.

Table 1. Origin and morphological description of genotypes used in the study.

Genotype	Origin	Characteristic
IAR-00-1074	Institute for Agricultural Research (IAR)	Dual-purpose, brown seed with rough seed coat, medium maturity (75 to 80 days), non-photosensitive.
IT93K-452-1	International Institute of Tropical Agriculture (IITA)	Grain-type. Medium white seeds, black hilum with rough seed coat, extra early maturity (55 to 60 days), erect, non-photosensitive.
IT93K-499-35	International Institute of Tropical Agriculture (IITA)	Grain-type white seeds, brown hilum with rough seed coat, early maturity (60 to 65 days), erect, non-photosensitive. Good grain yield. Multiple resistance to Striga strains.

(Tarawali et al., 1997). Cowpea fodder is as important as the grains, especially in the dry savannas, where, in the driest months of the year, cost of fodder per kg is as much as that of the grain (Langyintuo et al., 2003). The farmers wait until the cowpea leaves show signs of wilting before the cowpea are cut at the base and rolled into bundles with all leaves still intact. These bundles are kept on rooftops or in tree forks for drying and then sold in the peak dry season when prices are high. In case there are rains in October/November, the fodder type cowpea produce some grain as well. There is no evidence that any farmer can grow cowpea for fodder alone (Langyintuo et al., 2003). This suggests that, both grain and fodder are valuable. Therefore, the ratio of grain to fodder is very important to support the crop livestock integration system and adoption of varieties.

High level of genetic variation for the ratio of grain to fodder, otherwise known as dual-purposeness, exists in cowpea (Roquib and Patnaik, 1990). Variation exists for traits, such as the number of primary branches per plant, plant height, pod weight, leaf weight, branch weight, seed weight, threshing percentage, biomass, leaf stem ratio and harvest index. Understanding the genetic control of these traits will facilitate development of a viable breeding strategy for improved dual-purpose cowpea varieties with high grain and fodder yield. However, being a cleistogamous plant, production of hybrid cowpea remains economically nonviable for now. Therefore, a more detailed genetic study involving not only the F_1 generation but also advanced generations (F_2 and backcross) will be useful for a breeding program. Moreover, the genetic parameters is estimated mostly in Asia (Sharma and Singhania, 1992; Nehru and Manjunath, 2000; Mitra et al., 2001.), and that, being environment-specific, have limited use for the Nigerian cowpea belt. This suggests the need for a more comprehensive study of the genetic control of dual-purpose traits (days to first flower, plant height, pod

weight, leaf weight, branch weight, seed weight, biomass and fodder yield) in cowpea. The objective of the present study was to understand the gene action and inheritance patterns of dual-purpose traits and identify appropriate strategies for incorporation of these traits into the elite lines.

MATERIALS AND METHODS

Genetic materials

Parental pure lines were selected on the basis of their diversity and previously reported levels of fodder and grain production. The fodder type parent used was IAR-00-1074 and the grain type parents used were IT93K-452-1 and IT93K-499-35. The origin and morphological description of the genotypes used in this study are given in Table 1.

Crosses and generations

Crosses were made between fodder and grain type parents as follows: IAR-00-1074 x IT93K-499-35 and IAR-00-1074 x IT93K-452-1, generation mean analysis was performed using fodder type (P_1) and grain type (P_2) parents, F_1 and F_2 generations and backcrosses of the F_1 to each parent. All crosses were made by controlled pollinations in the greenhouse.

Experimental design

The six generations (P_1 , P_2 , F_1 , F_2 , BC_1 and BC_2) of each cross were grown in a randomized complete-block design with three replications during the rainy season of 2007 at the Institute for Agricultural Research (IAR) farm at Samaru (11°11'N; 07°38'E), in the Northern Guinea savanna ecological zone of Nigeria. Plot size varied for different families. Parental lines and the F_1 hybrids were grown in five-row plots, and the BC_1 , BC_2 and F_2 families were grown in 15-row plots, each of 3 m length. Recommended agronomic practices were followed throughout the crop season. Land was prepared by deep plowing, discing and harrowing. A basal fertilizer dose of 42 kg/ha N, 42 kg/ha P_2O_5 was applied one

month after germination, in the second week of September 2007. Insecticide (Decamethrin 2.5% W/V) and fungicide (Benomyl 50%) were sprayed at 10 days interval after emergence at the rate of 1 l/ha to control pests and diseases, respectively. In each replication, all observations were recorded on 15 randomly selected plants from the P₁, P₂ and F₁ generations, and 60 plants from the BC₁, BC₂ and F₂ families. Data were recorded on the following quantitative traits; days to first flower [taken as the number of days from sowing to first flower open (corolla visible)]; plant height as the height of the plant from soil surface to the tip of the main branch; dry leaf weight as the weight in gram of all the leaves on a plant; dry stem weight as weight of the dry shoot excluding the leaves of each plant; pod weight as weight of all dry pods on a plant; seed weight as dry seed weight in gram on per plants basis; total biomass as the weight of the dried leaves; dried pods, dried stems and dry fodder yield were measured as the weight of dried leaves plus the weight of dried stems.

Statistical analysis

Data collected were subjected to analysis of variance (ANOVA) to test for the equality of the means of the various populations in a cross using GenStat 5. (GenStat 5, 1993). To understand the distribution pattern of fodder yield in the various crosses, the field data were subjected to frequency analysis using 5% of the highest fodder yielding parents in the various populations as class range. The nature of dispersion, modal peaks and skewness observed were used to describe the nature of gene segregation for fodder yield.

The adequacy of the additive - dominance model was tested using the ABC scaling test (Mather, 1949), incorporating the weighted least square method of Hayman (1960) as follows:

$$A = 2\bar{B}_1 - \bar{P}_1 - \bar{F}_1$$

$$VA = 4V(\bar{B}_1) + V(\bar{P}_1) + V(\bar{F}_1)$$

$$B = 2\bar{B}_2 - \bar{P}_2 - \bar{F}_1$$

$$VB = 4V(\bar{B}_2) + V(\bar{P}_2) + V(\bar{F}_1)$$

$$C = 4\bar{F}_2 - 2\bar{F}_1 - \bar{P}_1 - \bar{P}_2$$

$$VC = 16V(\bar{F}_2) + 4V(\bar{F}_1) + V(\bar{P}_1) + V(\bar{P}_2)$$

$$S.E. (A) = (VA)^{1/2} \quad t(A) = A/S.E.(A)$$

$$S.E. (B) = (VB)^{1/2} \quad t(B) = B/S.E.(B)$$

$$S.E. (C) = (VC)^{1/2} \quad t(C) = C/S.E.(C)$$

Where, A, B and C are scaling test parameters, S.E. = standard error, V = variance, \bar{P}_1 , \bar{P}_2 , \bar{F}_1 , \bar{F}_2 , \bar{B}_1 , and \bar{B}_2 are the means of the fodder parent (P₁), and seed parent (P₂), their F₁, F₂ progeny, and progeny of the backcrosses of F₁ to P₁ and P₂, respectively.

The calculated values of t were compared with the tabulated values of "t" at 5 and 1% level of significance. In each test, the degrees of freedom are the sum of the degrees of freedom of the various generations involved (Mather, 1949). The significance of any one of these scales (that is, t-tests) was an indication of the presence of non-allelic interactions. If the additive-dominance model is adequate to explain the differences among generation means, C will be equal to zero within the limits of the standard error. When the additive-dominance model proved to be inadequate to

explain the variation existing among generations, the six-parameter model of Hayman (1958), Mather and Jinks (1971) incorporating mean [m], additive effect [d], dominance effect [h] and the three digenic interactive components, (additive x additive [i], dominant x dominant [j] and additive x dominant [ij]) was used as follows:

$$m = \bar{F}_2$$

$$d = \bar{B}_1 - \bar{B}_2$$

$$h = -\frac{1}{2}\bar{P}_1 - \frac{1}{2}\bar{P}_2 + \bar{F}_1 - 4\bar{F}_2 + 2\bar{B}_1 + 2\bar{B}_2$$

$$i = -4\bar{F}_2 + 2\bar{B}_1 + 2\bar{B}_2$$

$$j = -\frac{1}{2}\bar{P}_1 + \frac{1}{2}\bar{P}_2 + \bar{B}_1 - \bar{B}_2$$

$$l = \bar{P}_1 + \bar{P}_2 + 2\bar{F}_1 + 4\bar{F}_2 - 4\bar{B}_1 - 4\bar{B}_2$$

The significance of the genetic effects was tested using a similar t-test as for the ABC scaling test.

Broad-sense and narrow-sense heritability estimates were calculated using the methods of Mahmud and Kramer (1951) and Warner (1952), respectively.

RESULTS

Parent and progeny means

Significant differences were detected among generation means for all traits (Table 2). Means for parental, F₁, F₂ and backcross generations for the two crosses are listed in Tables 3 and 4. The fodder type parent (IAR-00-1074) had significantly higher mean performance compared to the grain types in both crosses for the measured traits. F₁ means were close to the means of the fodder parent for most traits. The F₁ means were significantly larger than the midparent values for pod weight, leaf weight, branch weight, seed weight, biomass and fodder yield in the cross IAR-00-1074 x IT93K-499-35. In the cross IAR-00-1074 x IT93K-452-1 (Table 4), the F₁ means were significantly larger than the midparent values for plant height, pod weight, leaf weight, branch weight, seed weight, biomass and fodder yield.

Frequency distribution for fodder yield for the cross IAR-00-1074 x IT93K-499-35 is shown in Figure 1. The F₁ showed a near bell-shaped distribution and a positive skew towards the fodder parent IAR-00-1074. The distribution of fodder yield in both backcrosses was similar and skewed towards their respective recurrent parents but continued to overlap. Five distinct modal phenotypic classes were observed in the F₂ distribution. The distribution was continuous in nature. There were transgressive segregates for fodder yield, with individual backcross and F₂ plants having values exceeding those of the fodder yield parent.

Similarly, the F₁ distribution for the cross IAR-00-1074 x IT93K-452-1 indicated a near bell-shaped distribution with a positive skew towards the higher fodder parent IAR-00-1074 (Figure 2). The distributions of fodder yield

Table 2. ANOVA for dual-purpose traits evaluated among generations in crosses IAR-00-1074 x IT93K499-35 and, IAR-00-1074 x IT93K452-1.

Trait	IAR-00-1074 x IT93K499-35		IAR-00-1074 x IT93K452-1	
	MS ^a	F _{calc} ^b	MS	F _{calc}
Days to first flower	1125.5	7.42***	202.9	21.5***
Plant height (cm)	5266.0	2.63*	11898.0	9.25***
Pod weight (g)	16931.2	19.56***	13648.0	11.43***
Leaf weight (g)	5128.9	33.88***	2016.0	13.33***
Branch weight (g)	5197.6	17.17***	1024.4	3.70***
Seed weight (g)	4887.9	20.74***	4653.0	15.57***
Biomass (g)	62456.0	26.42***	35514.0	11.93***
Fodder yield (g)	34059	23.10***	15529.0	8.99***

^aMS, Mean square; ^bF_{calc}, calculated F with 5 df (treatment) and 10 df (error); *,***significant differences at P<0.05 and P<0.0001 probability, respectively.

Table 3. Means of families derived from a cross involving IAR-00-1074 (fodder type) and IT93K-499-35 (grain type) of cowpea.

Population	Days to first flower	Plant height (cm)	Pod weight (g)	Leaf weight (g)	Branch weight (g)	Seed weight (g)	Biomass (g)	Fodder yield (g)
BC ₁	51	50.6	120.6	32.9	43.8	66.7	197.3	130.6
BC ₂	48	46.2	81.9	20.7	37.0	41.8	139.7	97.9
F ₁	47	52.1	107.5	32.8	41.9	58.3	182.2	123.8
F ₂	50	41.5	75.7	24.5	36.2	41.5	136.5	95.0
IAR-00-1074	52	85.5	104.9	35.6	44.6	53.5	185.1	131.6
IT93K-499-35	47	62.9	77.6	19.8	32.7	39.3	130.1	90.8
Mp	50	74.2	91.3	27.7	38.6	46.4	157.6	112.2
SE	0.40	0.63	12.40	2.84	2.96	3.85	10.60	7.53

SE, Standard error of mean; Mp, midparent value.

Table 4. Means of families derived from a cross involving IAR-00-1074 (a fodder type) and IT93K-452-1 (grain type) of cowpea.

Population	Days to first flower	Plant height (cm)	Pod weight (g)	Leaf weight (g)	Branch weight (g)	Seed weight (g)	Biomass (g)	Fodder yield (g)
BC ₁	50	72.1	65.1	32.8	42.3	37.4	140.2	118.9
BC ₂	45	77.3	74.8	23.4	39.6	39.7	137.7	92.5
F ₁	46	92.6	102.8	39.5	55.9	56.2	198.1	91.7
F ₂	48	86.4	79.4	29.8	45.4	40.1	154.6	120.9
IAR-00-1074	53	80.9	84.2	39.6	53.6	50.9	177.5	102.2
IT93K-452-1	42	79.3	51.4	15.8	27.4	28.4	94.6	66.0
Mp	48	80.1	67.8	27.7	40.5	39.6	136.0	85.0
SE	0.80	8.54	9.40	4.35	5.56	4.56	18.22	19.94

SE, Standard error of mean; Mp, midparent value.

in both backcrosses were similar and skewed towards the grain parent IT93K-452-1, and continued to overlap. The

F₂ population showed a bi-modal continuous distribution. However, there were no transgressive segregates for

Table 5. Estimates of genetic parameters for dual purpose traits for the cross IAR-00-1074 x IT93K-499-35.

Component	Days to first flower	Plant height (cm)	Pod weight (g)	Leaf weight (g)	Branch weight (g)	Seed weight (g)	Biomass (g)	Fodder yield (g)
[m]	50.0 ± 0.5**	41.0 ± 4.2**	76.0 ± 4.9**	25.0 ± 1.9**	36.0 ± 3.1**	58.0 ± 2.2**	137.0 ± 8.8**	95.0 ± 7.0**
[d]	3.0 ± 0.7**	5.0 ± 8.1	39.0 ± 9.8**	12.0 ± 2.9**	7.0 ± 3.9**	25.0 ± 5.0**	57.0 ± 5.6**	32.7 ± 11.2**
[h]	-4.5 ± 2.3**	7.5 ± 2.6**	117.5 ± 25.6**	13.0 ± 9.4**	21.0 ± 14.2**	-18.0 ± 3.4**	150.5 ± 3.9**	89.6 ± 33.0*
[i]	-2.0 ± 2.3	30.0 ± 3.2**	102.0 ± 27.7**	8.0 ± 9.6	18.0 ± 14.8**	46.1 ± 21.1*	126.0 ± 7.1**	77.0 ± 35.9*
[j]	0.5 ± 2.2	-6.5 ± 8.8	25.5 ± 33.5	4.0 ± 10.4	1.0 ± 13.1	15.0 ± 8.1*	29.5 ± 2.8**	12.3 ± 35.7
[l]	-3.0 ± 3.3	29.0 ± 8.8	-111.0 ± 45.3**	6.0 ± 14.6	-18.0 ± 20.7	-28.0 ± 23.2	-104.0 ± 116.0	-54.0 ± 54.2

m, Mean; d, additive effect; h, dominance; i, additive x additive; j, additive x dominance; l, dominance x dominance.

*, ** Estimate significantly different from zero at P = 0.05 or 0.01, respectively.

fodder yield in this cross.

Gene effects

The nature of gene action involved in the control of the measured traits was investigated by the analysis of generation means (Tables 5 and 6). The generation means analysis indicated that the additive-dominance model was not adequate to explain the gene action involved in the inheritance of the measured traits, except for days to first flower in both crosses and leaf weight in the cross (IAR-00-1074 x IT93K-499-35). The three-parameter model satisfactorily explained the genetic differences for days to first flower in both crosses. The additive [d] and dominance [h] components were significant for days to first flower. While additive gene action was in the direction of the fodder parent, the negative direction of the dominance gene action suggested that alleles were contributed by the respective grain parents for early maturity.

Significant dominance [h], additive x additive [i]

and additive x dominance [l] gene actions were detected for plant height in the IAR-00-1074 x IT93K-499-35 cross (Table 5). The gene actions were positive in the direction of the fodder parent. The additive x additive [i] and additive x dominance [l] effects were of equal magnitude. Similar trends were observed in the second cross (Table 6). The significant and positive dominance x dominance [l] gene action would suggest the presence of dominance effects at heterozygous loci for taller plants. For pod weight, the opposite sign of the dominance [h] and dominance x dominance [l] gene effects suggests duplicate gene action which would limit the range in variability and thus slow down the pace of progress through selection for this trait in both crosses.

Gene action for leaf weight in the cross IAR-00-1074 x IT93K-499-35 indicated that the additive [d] and dominance [h] gene effects were positive and of similar magnitude in the direction of the fodder parent (IAR-00-1074). However, for the cross IAR-00-1074 x IT93K-452-1 (Table 6), a more complex gene action in the form of a

significant positive additive [d] and dominance x dominance [l] gene effects in the direction of the fodder parent was indicated. The additive x additive [i] effect was negative in the direction of the grain type parent, IT93K452-1.

Significant positive additive [d], dominance [h], and additive x additive [i] gene actions were indicated for branch weight in the cross IAR-00-1074 x IT93K-499-35 (Table 5). However in the cross IAR-00-1074 x IT93K-452-1 (Table 6), the additive x additive [i] and additive x dominance [j] gene actions were in the direction of the grain parent. The significant and positive dominance x dominance [l] gene action would suggest dominance effects at heterozygous loci for larger branch weight in each parent.

For seed weight in the cross IAR-00-1074 x IT93K-499-35 (Table 5), the additive [d], additive x additive [i] and additive x dominance [j] effects were significant and positive toward the fodder parent. The dominance [h] gene action was in the direction of the grain type cowpea (IT93K-499-35). In the cross IAR-00-1074 x IT93K-452-1 (Table 6), the dominance x dominance gene action was in

Table 6. Estimates of genetic parameters for dual purpose traits for the cross IAR-00-1074 x IT93K-452-1.

Component	Days to first flower	Plant height (cm)	Pod weight (g)	Leaf weight (g)	Branch weight (g)	Seed weight (g)	Biomass (g)	Fodder yield (g)
[m]	48.0± 0.3**	86.0± 3.5**	79.0 ±1.0**	30.0± 0.8**	45.0± 1.4**	40.0± 1.0**	155.0± 3.3**	114.5± 2.7**
[d]	5.0±0.2**	-5.0± 4.6	-10.0± 3.0**	10.0± 1.3**	2.0 ± 1.3	-3.0 ± 1.6	2.0 ± 4.8	4.8 ± 3.7
[h]	-3.5± 1.5**	-33.0± 18.3	-0.5±8.8	3.0± 4.6	-1.5± 6.5	10.5± 6.0	-2.0 ± 18.1	-10.7± 14.31
[i]	-2.0 ±1.4	-46.0± 16.7**	-36.0± 7.2**	-8.0± 4.1**	-16.0± 6.0**	-6.0 ± 5.0	-64.0 ± 16.4**	-56.4± 13.2**
[j]	-0.5±1.2	-6.0± 14.8	-26.5 ±9.9**	-2.0± 4.5	-11.5± 3.2**	-14.5± 5.2**	-39.0± 15.3**	-25.2± 11.7*
[l]	-1.0± 2.2	94.0± 27.7**	97.0± 16.4**	30.0± 7.3**	45.0± 8.9**	43.0± 9.9**	176.0± 28.0**	131.0± 21.5**

m, Mean; d, additive effect; h, dominance; i, additive x additive; j, additive x dominance; l, dominance x dominance.

*, ** Estimate significantly different from zero at P = 0.05 or 0.01, respectively.

the direction of the fodder parent which would suggest dominance effects at heterozygous loci for seed weight in each parent.

For biomass, the additive [d], dominance [h], additive x additive [i] and dominance x dominance [l] genetic effects were significant and positive in the direction of the fodder parent in the cross IAR-00-1074 x IT93K-499-35 (Table 5). However, for IAR-00-1074 x IT93K-452-1 cross (Table 6), the additive x additive [i], additive x dominance [j] and dominance x dominance [l] gene interaction effects were significant

Significant and positive additive [d], dominance [h] and additive x additive [i] gene action were observed for fodder yield in the cross IAR-00-1074 x IT93K-499-35 (Table 5). The combined [d] + [i] component was larger than the dominance [h] component, suggesting that response to selection should be effective in early generations for fodder yield in this cross.

Heritability estimates varied considerably between crosses (Table 7). Broad-sense heritability (h^2_B) ranged from 0.21 to 0.98, and narrow-sense heritability (h^2_N) ranged from 0.12 to 0.62.

DISCUSSION

Differential performance of genotypes in segregating populations has often been used by geneticists to indicate the presence of heritable variation. The large degree of variation among the different populations for days to first flower, plant height, pod weight, leaf weight, branch weight, biomass and fodder yield strongly suggest the existence of genetic differences for these traits. Similar results have been reported for yield and related characters by Jatasara et al. (1982), Wein and Summerfield (1980), Tyagi et al. (1978), Sharma and Singhanian (1992), and Nehru and Manjunath, (2000), in fodder cowpea and by Rekha (1995) and Sharma (1999) in grain cowpea. In the two crosses considered in this study, the means of the parents (P_1 and P_2) showed a tendency to be more extreme and contrasting than the means of the F_1 and F_2 generations for the measured traits. The heritable differences that abound among the parents, offered an opportunity to elucidate the genetic nature of the inheritance for these traits.

The trend of means for various traits and crosses evaluated indicate that, for days to first flower, the fodder type parent IAR-00-1074 flowered later than the grain types. The parent IT93K-452-1 was the earliest flowering parent and had the least fodder yield (66 g per plant) compared to the fodder yielding parent IAR-00-1074 (102g per plant). IT93k-499-35 was intermediate in flowering time (47 day) and in fodder yield between the other two parents. This is indicative that in improvement efforts, incorporating a multi-trait such as high grain plus fodder yield into a single genotype is likely to be difficult in a short to medium growing season. The results indicate that with slight variation in maturity period, both grain and fodder yield can be improved. These findings are in agreement with Tyagi et al. (2000) who reported positive significant correlation between days to first flower and fodder yield. Akundabweni et al. (1990) also reported that lower total leaf fresh yields were associated with early to medium flowering in cowpea. The midparental values were larger than the F_1 mean for days to first flower in the crosses

Table 7. Estimates of heritability for dual-purpose traits derived from crosses IAR-00-1074 x IT93K-499-35 and IAR-00-1074 x IT93K-452-1.

Trait	IAR-00-1074 x IT93K-499-35		IAR-00-1074 x IT93K-452-1	
	h^2_B	h^2_N	h^2_B	h^2_N
Days to first flower	0.86	0.30	0.98	0.45
Plant height (cm)	0.28	0.14	0.21	0.12
Pod weight (g)	0.29	0.26	0.57	0.47
Leaf weight (g)	0.97	0.29	0.58	0.48
Branch weight (g)	0.69	0.21	0.83	0.39
Seed weight (g)	0.37	0.15	0.58	0.25
Biomass (g)	0.51	0.32	0.55	0.45
Fodder yield (g)	0.63	0.62	0.58	0.38

h^2_B and h^2_N are broad-sense heritability and narrow-sense heritability respectively.

studied (Tables 3 and 4), suggesting that dominance was in the direction of early maturity. This is further confirmed by the negative signs observed for the dominant component in the epistatic model. These observations are in agreement with the findings of Ojomo (1971) and Mak and Yap (1980) who reported dominance effects in the direction of earliness. However, this is in contrast with the findings of Ishiyaku et al. (2005), who reported partial dominance of late flowering. Based on results from the present study, population development in a breeding program should be initiated between medium and late maturing varieties.

The fodder parent IAR-00-1074 used in this study had higher plant height relative to the grain type (IT93K499-35). This also translated into higher biomass and fodder yields of the fodder parent which could suggest that the taller the plant, the heavier the biomass and fodder yield. These findings are in agreement with Tyagi et al. (1978), who reported a significant and positive correlation between plant height and fodder yield.

Mean pod weight, seed weight, leaf weight and branch weight were higher in the fodder parent relative to the grain types. This translated into heavier biomass and fodder yield. This observation is in agreement with those of Thaware et al. (1991) who reported a close association between branch weight per plant and fodder yield. There was an apparent association between the weights of the structural parts of the cowpea varieties and fodder yield used in this study. Such associations between foliar and structural components of green forage have been reported by Chopra and Singh (1977). However, in this study, to expect a positive association between the structural components and grain yield means that a given genotype must be able to partition its photosynthate to both the sink (grain) and source (vegetative component) in equal measure. The frequency distributions of the parents and their F_1 hybrids with respect to fodder yield confirmed the patterns shown by family means (Figures 1 and 2). The F_1 distributions were skewed towards that of

the fodder parent, suggesting that alleles for fodder yield in the fodder parent IAR-00-1074 are dominant. The distributions of the segregating F_2 populations in the crosses imply that fodder yield is governed by polygenes. Quantitative inheritance of fodder yield has been reported. Tyagi et al. (2000), in a study of the component analysis of green fodder yield in cowpea, noted that fodder-yield is a very complex trait that is influenced by many factors. Grafius (1956) also stated that, to develop high-yielding cowpea genotypes, selection based on yield alone will not be very effective unless due emphasis is given to fodder components. The BC_1 and BC_2 frequency distribution skewed towards their respective recurrent parents (Table 6) and their overlapping nature confirms the presence of epistatic interactions between genes. Similar trends were observed by Audilakshmi and Aruna, (2005), although in sorghum. The frequency distribution of the backcross in the cross IAR-00-1074 x IT93K-452-1 was skewed towards the lower fodder yielding parent IT93K-452-1. This suggests that there may be a high concentration of low fodder yielding genes in IT93K-452-1.

The transgressive segregates observed in the cross IAR-00-1074 x IT93K-499-35 for fodder yield suggest that the fodder yielding genes are dispersed among the parents; however, in the cross IAR-00-1074 x IT93K-452-1, there were no transgressive segregates for fodder yield, indicating that the fodder yielding genes are not dispersed among the parents and that all genes for high fodder yield are in one parent and those for low fodder yield are in the other parent.

Gene action and empirical estimates of genetic parameters governing trait expression is useful in developing strategies for incorporating genes. For the cross IAR-00-1074 x IT93K-499-35, dominance gene action had the greatest magnitude of any single effect for all traits except for plant height and seed weight and was mostly positive towards the fodder parent. The additive [d], dominance [h] and additive x additive effects were nearly

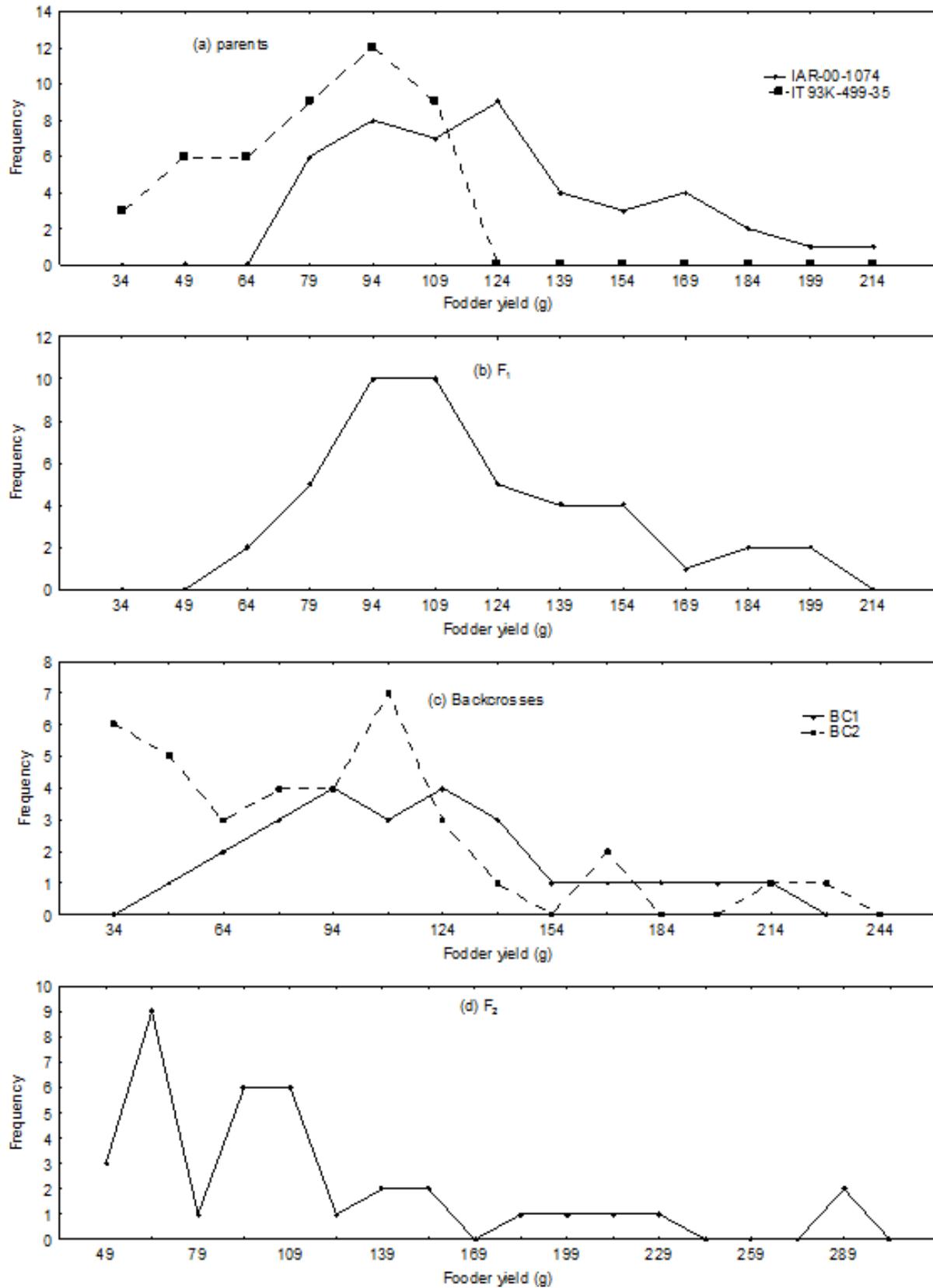


Figure 1. Frequency distribution of fodder yield per plant in cowpea for a) parents; b) F₁; c) backcrosses; and d) F₂ populations for the cross IAR-00-1074 X IT93K-499-35.

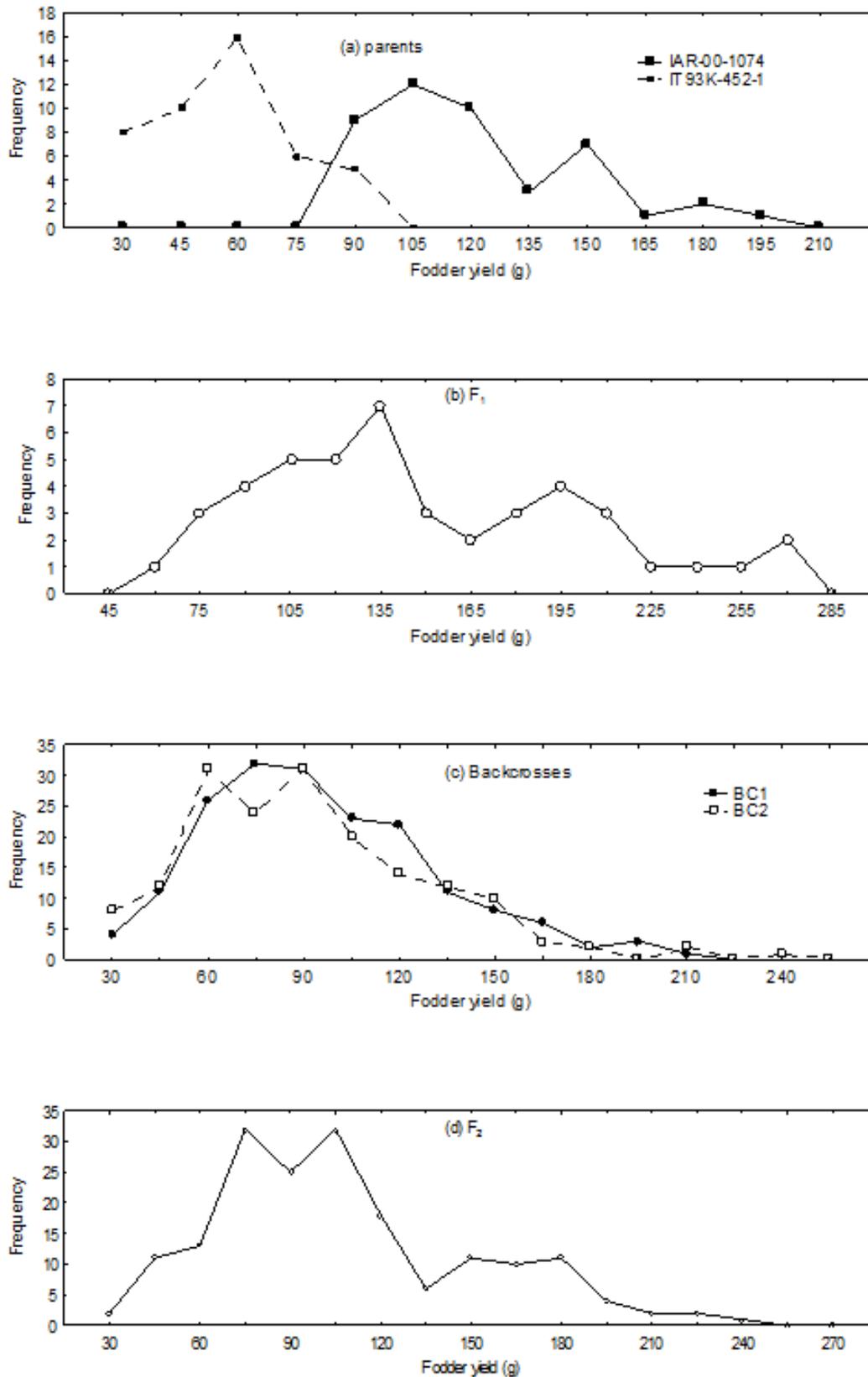


Figure 2. Frequency distribution of fodder yield per plant in cowpea for; a) parents; b) F₁; c) backcrosses; d) F₂ populations for the cross IAR-00-1074 X IT93K-452-1.

always positive for all measured traits. However, the sum of significant additive and additive x additive [i] gene effects was usually of greater magnitude compared with the sum of the significant dominance [h] and dominance x dominance [j] effects. This suggests that there is considerable amount of additive variation for the measured traits in this cross which should favor selection in early generations for improvement of the measured traits. For the cross IAR-00-1074 x IT93K-452-1, the dominance x dominance gene effect had the greatest magnitude of any single effect and was mostly positive toward the fodder parent for all measured traits. The sum of significant dominance [h] and dominance x dominance [j] gene effects was usually of greater magnitude compared with the sum of the significant additive [d] and additive x additive [i] effects. Significant estimates of additive effect ([d] and [i]) were usually negative in contrast to the significant gene effects ([d] and [dd]) which were usually positive. The contrasting gene action from the two populations suggests that the two grain type parents differ in gene action for the measured traits.

The results for days to first flower are in contrast with the results obtained by Ishiyaku et al. (2005), who noted significant additive [d] and additive x dominance [j] gene effects for time to first flower in a cross between photo-insensitive and photo-sensitive cowpea. However, only photo-insensitive cowpeas were used in this present study. Plant height was predominantly under duplicate gene action in the cross IAR-00-1074 x IT93K-452-1. However, in the cross IAR-00-1074 x IT93K-499-35, it was under complementary gene action. Similar results was reported by Audilakshmi and Aruna, (2005). The prevalence of duplicate gene action would limit selection in early generations for plant height. It may therefore be necessary to delay selection in early selfing generations until homozygosity is reached. Pod weight was predominantly under duplicate gene action in both crosses. These observations are in agreement with those reached by Pathamanathan et al. (1997), who reported that although both additive [d] and dominance [h] effects were statistically significant, additive effects were larger and of more importance in the inheritance of pod weight.

Leaf weight, biomass and branch weight were also predominantly under duplicate gene action. However, seed weight was predominantly under complementary gene action in this study, suggesting the possibility of considerable amount of heterosis for seed weight. This is in agreement with the finding of Arvindhan and Das (1996). Fodder yield has been reported by many workers to be a complex trait influenced by many factors (Grafius, 1956; Mitra et al., 2001; Tyagi et al., 2000). The magnitude of the epistatic components [i, l and j] for fodder yield in this study suggests that their contribution to the inheritance of fodder yield is greater than that of the additive effects, but less than that of the dominant effects. Of the individual digenic effects, the dominance x

dominance [l] epistatic effect was of larger magnitude, further confirming the complexity of fodder yield.

The generally low estimates of broad and narrow-sense heritability indicate that the environment in which the plants were tested had a larger effect on the measured traits than the genotype. Breeding efforts to improve dual-purpose traits would require good control over the environmental variation.

Conclusion

In breeding self-pollinated species, the plant breeder seeks to produce an improved pure line. The purpose of hybridization is therefore, to provide genetic variation on which selection can act. Epistasis is more important than dominance to the breeder of self-pollinating species, because dominance is broken by segregation following hybridization. Epistasis, on the other hand, does not depend on heterozygosity and can therefore permit more gene combinations than dominance. Because dominance and epistasis made large contributions to the inheritance of dual-purpose traits in this study, rapid advances would best be made using a procedure, which emphasizes these gene effects. Since improved inbred lines are the desired product, selection should not be too severe in the early stages to allow for the desirable gene recombination. For genetic improvement of dual-purpose traits utilizing non-additive components, intermating among selected segregates in early generations, or reciprocal recurrent selection would be effective approaches.

REFERENCES

- Akundabweni LS, Peter-Paul C, Singh BB (1990). Evaluation of elite lines of cowpea (*Vigna unguiculata* (L.) Walp) for leaf fodder plus grain (that is, dual purpose). *Trop. Agric.* 67(2): 133-136.
- Arvindhan S, Das LDV (1996). Heterosis and combining ability in fodder cowpea for green fodder and seed yield. *Madras Agric. J.* 83: 11-14.
- Audilakshmi S, Aruna C (2005). Genetic analysis of physical grain quality in sorghum. *J. Agric. Sci.* 143: 267-273.
- Bressani R (1985). Nutritive value of cowpea, in: Singh SR, Rachie KO (Eds.). *Cowpea Research, Production and utilization*. John Wiley & Sons, New York, USA, pp. 353-360.
- Chopra SK, Singh C (1977). Correlation and path coefficient analysis in fodder cowpea (*Vigna unguiculata* [L.] Walp). *Forage Res.* 2: 97-100.
- Genstat 5 (1993). *GENSTAT 5 Reference manual*. Oxford: Clarendon Press.
- Grafius JE (1956). Components of yield in oat. A geometrical interpretation. *Agron. J.* 48: 419-423.
- Hayman BI (1958). The separation of epistatic from additive and dominance variation in generation means. *Heredity* 12: 371-390.
- Hayman BI (1960). Maximum likelihood estimates of genetic components variation. *Biometrics*, 16: 369-381.
- Ishiyaku MF, Singh BB, Craufurd PQ (2005). Inheritance of time to flowering in cowpea (*Vigna unguiculata* [L.] Walp) *Euphytica*, 142: 291-300.
- Jatasara DS, Gupta PC, Singh K (1982). Studies on forage production potential and quality of different varieties of cowpea. *Forage Res.* 8: p. 141.
- Langyintuo AS, Lowenberg-DeBoer J, Faye M, Lambert D, Ibro G,

- Moussa B, Kergna A, Kushwaha S, Musa S and Ntoukam G (2003). Cowpea supply and demand in West and Central Africa. *Field Crops Res.* 82: 215-231.
- Mahmud K, Kramer H (1951) Segregation for yield, height, and maturity following a soyabean cross. *Agron. J.* 43: 605-609.
- Mak C, Yap TC (1980). Inheritance of seed protein content and other agronomic characters in long bean (*Vigna sesquipedalis foww.*). *Theor. Appl. Genet.* 56: 233-239.
- Mather K (1949). *Biometrical Genetics*. Dover publication, Inc. New York.
- Mather K, Jinks JL (1971). *Biometrical Genetics*. Chapman and Hall Ltd., London.
- Mitra J, Natarajan S, Jain RK (2001). Gene action for fodder yield and its components in clusterbean (*Cyamopsis tetragonoloba* (L.) Taub). *Ind. J. Genet. Plant Breed.* 61(3): 253-255.
- Nehru SD, Manjunath A (2000). Genetic variability for yield and accessory characters in cowpea (*Vigna unguiculata* [L.] Walp). *Ind. Agric.* 45: 99-101.
- Ojomo OA (1971). Inheritance of flowering date in cowpea. [(*Vigna unguiculata* [L.] Walp).] *Trop. Agric. (Trinidad)*, 48: 277-282.
- Pathamanathan U, Ariyanagam RP, Hague SO (1997). Genetic analysis of yield and its components in vegetable cowpea, (*Vigna unguiculata* [L.] Walp). *Euphytica*, 96(2): 207-213.
- Rekha M (1995). Genetic variability studies in cowpea. *Madras Agric. J.*, 82: 150-152.
- Roquib MA, Patnaik RK (1990). Genetic variability in forage yield and its components in cowpea, (*Vigna unguiculata*). *Environ. Ecol.* 8: 236-238.
- Sharma TR (1999). Genetic variability studies in cowpea. *Legume Res.* 22: 65-66.
- Sharma CD, Singhania DL (1992). Performance of cowpea genotypes for fodder traits. *Ann. Arid Zone* 31: 65-66.
- Tarawali S, Singh BB, Peters M, Blade SF (1997). Cowpea haulms as fodder. In: Singh BB, Mohan Raj DR, Dashiell, KE, Jackai LEN (Eds.). *Advances in cowpea research*, International Institute of Tropical Agriculture (IITA), and Japan International Research Center for Agricultural Sciences (JIRCAS). Ibadan, pp. 313-325.
- Thaware BL, Birari SP, Jamadagni BM (1991). Genetic Parameters and Correlation studies in forage yield components of cowpea. *J. Maharashtra Agric. Univ.* 16(2): 261-262.
- Tyagi PC, Kumar N, Agarwal MC (2000). Genetic variability and association of component character for seed yield in cowpea. *Legume Res.* 23: 92-96.
- Tyagi ID, Parihar BPS, Dixit RK, Singh HG (1978). Component analysis of green fodder yield in cowpea. *Ind. J. Agric. Sci.* 48: 646-649.
- Warner JN (1952). A method for estimating heritability. *Agon. J.* 44: 427-430.
- Wein HC, Summerfield RJ (1980). Adaptation of Cowpea in West Africa: Effects of photoperiod and temperature responses in cultivars of diverse origin. In: Summerfield, R.J., Bunting, A.H., (Eds), HMSO. London, *Adv. Legume Sci.* pp. 405-417.